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Benthic polychaete diversity patterns and community structure in the Whittard Canyon system and adjacent slope (NE Atlantic)

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ABSTRACT

We examined deep-sea macrofaunal polychaete species assemblage composition, diversity and turnover in the Whittard Canyon system (NE Atlantic) using replicate megacore samples from three of the canyon branches and one site on the continental slope to the west of the canyon, all at ~3500 m water depth. A total of 110 polychaete species were recorded. *Paramphinome jeffreysii* was the most abundant species (2326 ind. m^{-2}) followed by *Aurospio* sp. B (646 ind. m^{-2}), Opheliidae sp. A (393 ind. m^{-2}), *Prionospio* sp. I (380 ind. m^{-2}), and *Ophelina abranchiata* (227 ind. m^{-2}). Species composition varied significantly across all sites. From west to east, the dominance of *Paramphinome jeffreysii* increased from 12.9% on the slope to 39.6% in the Eastern branch. Ordination of species composition revealed that the Central and Eastern branches were most similar, whereas the Western branch and slope sites were more distinct. High abundances of *P. jeffreysii* and Opheliidae sp. A characterised the Eastern branch of the canyon and may indicate an opportunistic response to a possible recent input of organic matter inside the canyon. Species richness and diversity indices were higher on the slope compared with inside the canyon, and the slope site had higher species evenness. Within the canyon, species diversity between branches was broadly similar. Despite depressed diversity within the canyon compared with the adjacent slope, the fact that 46 of the 99 polychaete species found in the Whittard Canyon were not present on the adjacent slope suggests that this feature may enhance the regional species pool. However, our sampling effort on the adjacent slope was insufficient to confirm this conclusion.

1. Introduction

Describing and understanding patterns of biodiversity on our planet is a fundamental aim in biology (Gaston, 2000). The deep-sea floor may harbour some of the highest levels of local (alpha) species diversity on earth (Hessler and Sanders, 1967; Sanders, 1968; Sanders and Hessler, 1969; Grassle and Maciolek, 1992). A parabolic pattern of local diversity with water depth, with peaks at intermediate (i.e. mid to lower bathyal) depths and reduced diversity at upper bathyal and abyssal depths, is evident among some macrofaunal taxa, including polychaetes, in intensively studied areas of the North Atlantic (Rex, 1981; Rex, 1983; Etter and Grassle, 1992; Levin et al., 2001; Rex and Etter, 2010; Paterson and Lambshead, 1995). However, this pattern may not be a universal phenomenon across different taxa and deep-sea regions (Stuart et al., 2003; Stuart and Rex, 2009).

Submarine canyons, major deep-sea topographic features incising the continental shelf and slope, are among the potential exceptions to this pattern. They may show either increased species richness in their deeper parts (Cunha et al., 2011) or depressed diversity due to strong dominance, as in shallow parts (100 m depth) of the La Jolla Canyon system, which is influenced by significant macrophyte detritus input (Vetter and Dayton, 1998). Faunal diversity also varies down the canyon axis and across the adjacent canyon fan (Tyler et al., 2009), as reported for foraminifera in the Whittard Canyon (Duros et al., 2011) and polychaetes in the Nazaré, Setúbal and Cascais Canyons on the Iberian Margin (Paterson et al., 2011). There is, however, no general agreement on whether alpha diversity is typically higher inside canyons (Vetter and Dayton, 1998, 1999; Vetter et al., 2010; De Leo et al., 2012) or higher on the adjacent slope outside canyons (Gage et al., 1995; Curdia et al., 2004; Garcia et al., 2007; Koho et al., 2007).

The drivers that influence marine diversity at regional and local scales are not well understood (Levin et al., 2001; Snelgrove and

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Smith, 2002). In the case of submarine canyons, a complex interplay of numerous factors is likely to regulate the diversity of biological communities (McClain and Barry, 2010). These topographic features are typically associated with high surface water productivity, high levels of physical disturbance and a considerable degree of habitat heterogeneity, all of which could influence species diversity. Canyons have also been described as benthic biomass 'hotspots' (Vetter, 1994; De Leo et al., 2010), reflecting an enhanced food supply compared with the surrounding continental slope and abyssal plain. They can act as conduits for the delivery of sediment and organic matter to the abyssal plains (Vetter and Dayton 1998). This enhanced supply of organic matter could increase diversity. Conversely, if enrichment is excessive, it may favour opportunistic species (Paterson et al., 2011) and act to depress species diversity (Stuart et al., 2003; Whittaker, 1965), as in the Nazaré Canyon (Curdia et al., 2004). Diversity may also be influenced by physical disturbance, for example, when steep topography focuses internal tides in the upper reaches of canyons (Gardner, 1989), while tidal currents, episodic slumps, turbidity flows and dense shelf water cascading may periodically transport sediments into the deeper parts (Shepard, 1951; Canals et al., 2006).

Factors such as extreme topography, diverse current regimes, varying substratum types, and detrital funnelling from the continental shelf serve to increase habitat heterogeneity within canyons (Levin et al., 2010). For example, currents may distribute organic matter and sediment in a patchy manner (McClain and Barry, 2010). Similarly, sediment granulometry can be expected to vary throughout a canyon, with potential impact on macrofaunal (Etter and Grassle, 1992) and meiofaunal (Leduc et al., 2012) diversity. Sessile megafauna add to the habitat complexity inside canyons; they include deep-water corals that are found in many canyon systems and provide refuge for diverse associated faunal communities (Mortensen and Buhl-Mortensen, 2005; Buhl-Mortensen et al., 2010; Huvenne et al., 2011). All of these factors may increase small and medium-scale environmental heterogeneity, particularly within active canyons, and thereby enhance diversity compared with the adjacent slope (Tews et al., 2004). Indeed, increased macrohabitat heterogeneity inside canyons has been linked to the high beta diversity of nematode assemblages (Vanreusel et al., 2010).

On a larger scale, it is unclear whether canyons act to enhance regional diversity across continental margins. Evidence from canyons in the Hawaiian Archipelago suggest that they lead to an increase in megafaunal (Vetter et al., 2010) and macrofaunal (De Leo et al., 2014) species turnover (beta diversity). Beta diversity links local and regional scales of diversity and has been understudied in deep ocean settings (Paterson et al., 1998; Glover et al., 2002; Ellingsen et al., 2007a). In deep-sea, soft-sediment habitats, variation in beta diversity is expected to be gradual except when interrupted by topography, hard substratum, intense bottom currents, nutrient depo-centres, abrupt shifts in water masses, or other extreme environmental circumstances (Rex and Etter, 2010). Many of these factors operate inside canyons. Thus, as in continental shelf settings (Ellingsen and Gray, 2002), it seems likely that changes in environmental variables within canyons will have a stronger effect on beta diversity than spatial distance between sites. The bathymetric and geographical ranges of species, and hence beta diversity, are influenced by the interplay between adaptive traits and environmental drivers. Adaptive traits include feeding type, metabolic and locomotory capacity, morphological specialisation, larval dispersal, adult mobility, body size and shape, and enzymatic pressure sensitivity (reviewed by Rex and Etter, 2010). Those traits typical of canyon settings will depend on the species present, which in turn will reflect the environmental conditions. Thus the interaction of species traits and environmental influences that determine the bathymetric and geographical ranges of species will be complex (Rex and Etter, 2010). Since the environmental conditions inside canyons are often very different from those on the open slope, the faunal assemblages may differ correspondingly. This would act to increase faunal turnover across the continental margin and lead to enhanced regional diversity.

Much less quantitative data on species richness is available from deep-sea soft sediments than from comparable shallow-water settings (Gray, 2002). As a result of their rugged terrain and inaccessibility, submarine canyons are particularly hard to sample. Thus, relatively little is known about the patterns and drivers of canyon diversity. This study will investigate diversity inside the Whittard Canyon system (NE Atlantic), focussing on sites at a common water depth (3500 m). A previous study, on the same samples from the Whittard Canyon, reported macrofaunal abundance and community composition at the higher taxon level (Gunton et al., 2015).

In the present study, a species-level assessment of polychaete assemblages, typically the dominant deep-sea macrofauna taxon, will be used to address the following hypotheses. (1) Species composition is not consistent between Whittard Canyon branches. (2) Species composition for the canyon site as a whole (including all three branches) is different from that of the slope site. (3) Species diversity is depressed inside the Whittard Canyon as a whole compared with the slope site. (4) Regional diversity is enhanced by the Whittard Canyon system.

2. Methods

2.1. Sample collection and processing

Sediment samples were collected using a Megacorer (Gage and Bett, 2005) at three sites inside the Whittard Canyon system (NE Atlantic) and one on the adjacent continental slope to the west of the canyon during RRS *James Cook* cruise 036 in June and July 2009 (Table 1; Fig. 1). All sites were located at ~3500 m depth. The Megacorer was fitted with eight large (100 mm internal diameter) core tubes. For one deployment at each site one of the larger core tubes was replaced with a single smaller tube (59 mm internal diameter) (Table 1). Five deployments were conducted in the Western branch, six in the Central and Eastern branches and five at the slope site. One extra deployment was made in the Central and Eastern branches to compensate for the failure to recover sufficient cores. Core slices from the same sediment layer from one deployment were pooled to make one replicate sample. The number of cores pooled per deployment ranged from 3 to 7 and the area of seabed sampled varied accordingly (Table 1). Samples were fixed with 10% borax-buffered formalin. Full details of macrofaunal sample processing are given in Gunton et al. (2015). In the present study, the top three sediment horizons (i.e. 0–1, 1–3 and 3–5 cm) were analysed *in toto*.

2.2. Faunal analyses

In the laboratory, polychaetes were transferred from the formalin onto a 300 μm mesh sieve, rinsed with fresh water and sorted in 70% ethanol. A Leica MZ9.5 stereomicroscope and a DM5000 compound microscope were used to identify polychaete specimens to species level. Polychaetes were assigned a Latin binomial name where possible using published identification keys. Where specimens could not be assigned to a described species they were recorded as an informal morphospecies in a genus (e.g. *Prionospio* sp. A) or family (e.g. Spionidae sp. A). Fragmented specimens were only counted if they included a head. The full

Table 1
Sites and diversity summary.

Deploy.	Lat. (N)	Long. (W)	Depth (m)	Cores recovered	Area (m^{-2})	Density (ind. m^{-2})	Total species	J'	H' (log2)	$1-\lambda'$	Rank 1 dom. (%)	Chao 1
Sl016	47° 56.79′	10° 46.85′	3511	8	0.063	939	21	0.876	3.848	0.902	22.6	38.81
Sl017	47° 56.78′	10° 46.85′	3512	7	0.055	982	23	0.923	4.175	0.932	13.7	35.91
Sl018	47° 56.81′	10° 46.91′	3514	6	0.047	1358	28	0.885	4.253	0.927	15.9	64.80
Sl019[a]	47° 56.74′	10° 46.94′	3505	8	0.063	1337	30	0.857	4.207	0.920	18.5	50.10
Sl020	47° 56.78′	10° 46.85′	3514	7	0.055	1364	25	0.870	4.039	0.910	23.0	32.68
Ave. Sl							**25.4**	**0.882**	**4.104**	**0.918**	**18.7**	**44.46**
W002[a]	48° 09.18′	10° 33.70′	3670	8	0.063	1226	22	0.800	3.567	0.870	26.7	34.18
W003	48° 09.17′	10° 33.70′	3661	7	0.055	1328	22	0.818	3.646	0.875	27.9	39.03
W011	48° 09.22′	10° 32.36′	3582	6	0.047	1422	24	0.861	3.949	0.905	20.3	37.58
W026	48° 09.18′	10° 33.73′	3670	5	0.039	1223	19	0.891	3.784	0.904	19.1	24.87
W043	48° 09.15′	10° 33.76′	3657	6	0.047	1443	23	0.792	3.582	0.848	34.4	47.59
Ave. W							**22.0**	**0.832**	**3.706**	**0.880**	**25.8**	**36.65**
C063[a]	48° 16.89′	10° 18.74′	3375	6	0.047	1995	25	0.748	3.474	0.799	42.7	29.67
C064	48° 16.97′	10° 18.65′	3382	8	0.063	2388	34	0.762	3.877	0.850	35.6	33.71
C065	48° 17.04′	10° 18.89′	3373	7	0.055	2165	36	0.810	4.187	0.887	29.8	42.41
C067	48° 16.98′	10° 18.72′	3376	7	0.055	1528	27	0.791	3.761	0.854	34.2	39.35
C066	48° 16.83′	10° 18.72′	3381	3	0.063	2308	37	0.798	4.155	0.891	27.1	33.28
C068	48° 17.01′	10° 18.83′	3375	5								
Ave. C							**31.8**	**0.782**	**3.891**	**0.856**	**33.9**	**35.68**
E093[a]	48° 15.89′	10° 09.56′	3424	8	0.063	1942	35	0.723	3.709	0.797	43.6	42.06
E094	48° 15.78′	10° 09.57′	3429	7	0.055	2583	33	0.762	3.842	0.845	36.2	35.91
E095	48° 15.78′	10° 09.58′	3429	4	0.063	3184	43	0.712	3.866	0.821	40.1	40.22
E096	48° 15.76′	10° 09.60′	3424	4								
E097	48° 15.89′	10° 09.54′	3425	5	0.039	4304	29	0.662	3.214	0.764	45.2	28.93
E098	48° 15.76′	10° 09.60′	3432	4	0.031	4330	32	0.730	3.652	0.843	33.6	39.78
Ave. E							**34.4**	**0.718**	**3.656**	**0.814**	**39.7**	**37.38**

[a] Deployment where sample for sediment grain-size analysis was collected. Ave.=mean of five deployments. J', Pielou's evenness; H' (log2), Shannon index; $1-\lambda'$, Simpson index; Chao 1 values rarefied to 47 individuals.

species list, including abundance counts, is given as supplementary data (Table S1).

2.3. Data analysis

2.3.1. Diversity measures

Simple polychaete species dominance was calculated as the Berger–Parker index (i.e. Rank 1 Dominance; Magurran, 2004). K-dominance plots (Lambshead et al., 1983) were drawn in SigmaPlot V12.5. The software package PRIMER V6 (Clarke and Gorley, 2006) was used to calculate conventional diversity indices from the polychaete count data: Shannon index (Pielou, 1966), Simpson's index (Simpson, 1949) and Pielou's evenness (Pielou, 1975). Rarefied polychaete species richness ($E[S_{47}]$) was estimated based on values derived from individual-based rarefaction curves (Gotelli and Colwell, 2001, 2011). The rarefaction curves based on polychaete count data were constructed using the EstimateS software package (Colwell, 2009). This approach was also applied to comparative polychaete species-level data available from canyons on the Iberian Margin (Paterson et al., 2011). Finally, species richness was estimated using values of Chao 1 from the EstimateS output.

In order to assess beta diversity across the canyon system, Whittaker's measure $\beta_W=\gamma / \bar{\alpha}$ (Whittaker, 1960, 1972) was calculated, where γ is the diversity of the complete system (i.e. all relevant sites combined), and $\bar{\alpha}$ is average sample diversity, where each sample is of a standard size (i.e. by rarefaction). Beta diversity was calculated using the number equivalents (Hill numbers) of species richness ${}^0D=S$, Shannon index ${}^1D=\exp(-\Sigma_{pi} \log_{pi})$ and Simpson index ${}^2D=1/\Sigma_{pi}{}^2$ (See Chao et al., 2012, 2014a; Jost, 2007), derived from the output of EstimateS, after individual samples had been rarefied to 47 individuals and pooled samples (the γ value) rarefied to 235 individuals (i.e. 5 replicate samples of 47 individuals). We adopted this approach following the rationale of Chao et al. (2014b), where the use of Hill number diversity values simplifies the calculation of reasonable beta diversity values. Similarly, we assess ${}^0D$, ${}^1D$ and ${}^2D$ to examine the potential variation in richness, heterogeneity, and dominance aspects of beta diversity, according to the general framework proposed by Chao et al. (2014b).

2.3.2. Composition assessment

Polychaete species density data were transformed to square root, and the Bray–Curtis similarity calculated between samples. The resultant similarity matrix was visualised using non-metric multidimensional scaling plots (nMDS plots), and further assessed using the Analysis of Similarity (ANOSIM) and Similarity Percentage (SIMPER) methods given in PRIMER V6.

A canonical correspondence analysis (CCA) on untransformed polychaete density was performed to examine the potential relationships between assemblages and environmental variables. The CCA was performed using R statistical software (RCoreTeam, 2014) with the Vegan: Community Ecology package (Oksanen et al., 2013). Details of environmental variables used and their measurement, are given in Gunton et al. (2015). Briefly – a post-processed bathymetry map of the Whittard Canyon was downloaded from the INFROMAR website (www.gsiseabed.ie). Using the software ArcMap 10 (ESRI) and the Benthic Terrain Modeler ArcGIS Desktop Extension alpha version (Wright et al., 2005), the following environmental descriptors were derived from the bathymetry map; 'Slope', bathymetric position index (BPI) and vector ruggedness measure (VRM). Sediment particle-size was obtained from the smaller cores collected at each site (see Section 2.1). Subsamples from the 0–0.5, 1–1.5, 2–3 and 4–5 cm sediment layers from each core were analysed using a Malvern Mastersizer

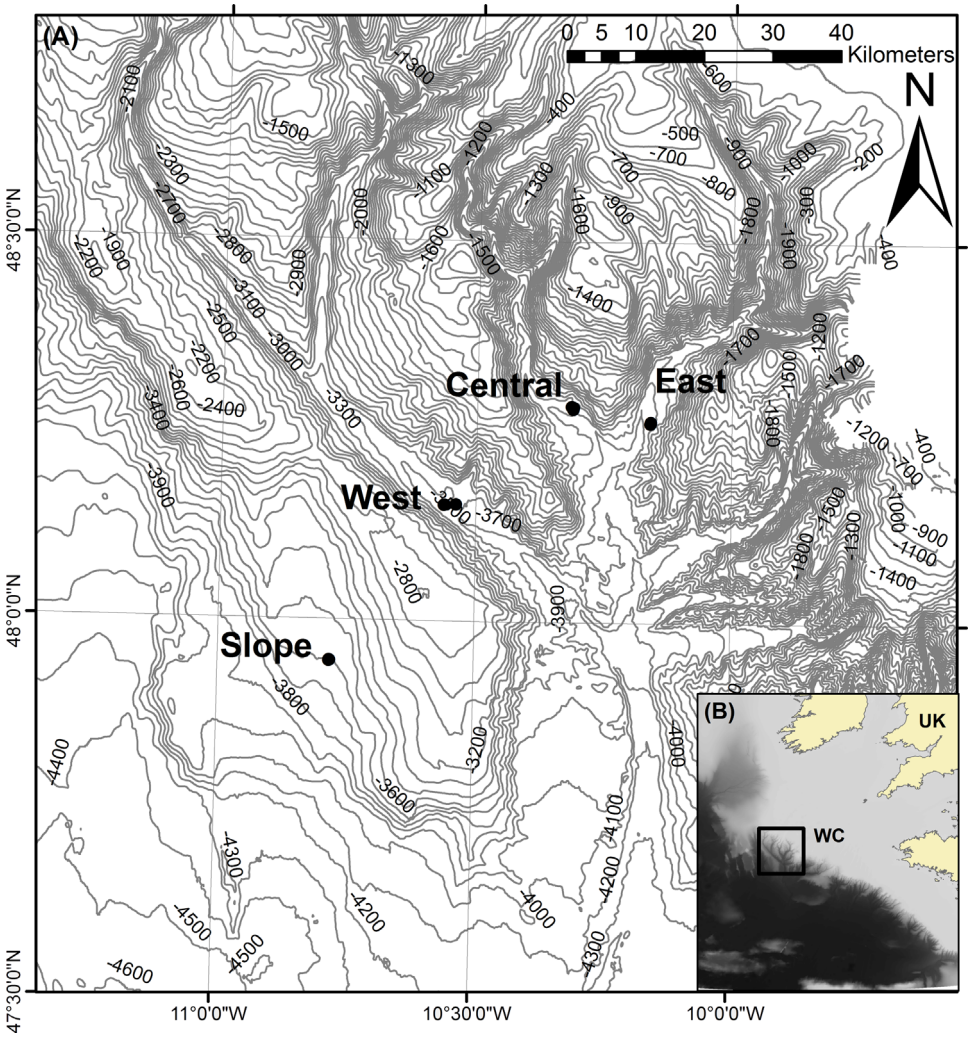

Fig. 1. (A) Bathymetric chart of Whittard Canyon, based on data provided by the Geological Survey of Ireland (www.gsiseabed.ie). The four study sites are indicated: Western Branch, Central Branch and Eastern Branch of the canyon and one site on the adjacent slope. (B) Location map of Whittard Canyon (WC) in NE Atlantic, based on GEBCO data (www.gebco.net).

2000 laser diffraction particle size analyser (Abbireddy and Clayton, 2009).

3. Results

3.1. The polychaete assemblages

In total, 2225 polychaetes were examined; 1959 (88%) of these were assigned to species, the remainder being considered as indeterminate. Across all sites, we recognised 110 species, of which 35 were described, and 75 could not be assigned to a known species and were possibly new to science. The Eastern branch yielded the highest number of species (68), followed by the Central branch (65), slope (64) and Western branch (53) sites. Overall, 46 species were found only in the canyon branches, and 11 were found only at the slope site. Among the 10 top-ranked species at each site (Table 2) (21 species in total), 3 were found only on the slope, 11 only in the canyon and 7 in both settings. Between site

Table 2
Top ten most abundant species at each site. Relative abundance shown in brackets.

Slope	Western branch	Central branch	Eastern branch
Aurospio sp. B (14.3%)	*Paramphinome jeffreysii* (21.2%)	*Paramphinome jeffreysii* (33.6%)	*Paramphinome jeffreysii* (39.6%)
Paramphinome jeffreysii (12.9%)	*Aurospio* sp. B (11.2%)	*Aurospio* sp. B (8.3%)	Opheliidae sp. A[a] (11.0%)
Anguillosyllis capensis (9.3%)	*Ancistrosyllis* sp. A[a] (10.2%)	*Ophelina abranchiata* (4.9%)	*Prionospio* sp. I (5.5%)
Prionospio sp. I (7.1%)	*Levinsenia gracilis* (6.5%)	*Levinsenia gracilis* (3.8%)	*Aurospio* sp. B (5.5%)
Aurospio dibranchiata (6.3%)	*Prionospio* sp. I (6.0%)	*Chaetozone* sp. F (3.4%)	*Leitoscoloplos* sp. B[a] (2.2%)
Flabelligella cf. biscayensis (5.4%)	*Leanira hystricis* (3.9%)	*Ophelina cylindricaudata* (3.3%)	*Ophelina abranchiata* (2.1%)
Ampharetidae sp. A (4.7%)	*Ophelina abranchiata* (3.8%)	Polychaeta larva sp. A[a] (3.0%)	*Glycera capitata* (2.0%)
Glycera capitata (3.4%)	*Chaetozone* sp. F (3.1%)	*Aurospio dibranchiata* (2.8%)	*Aricidea simplex* (1.8%)
Chaetozone sp. F (3.4%)	*Chaetozone* sp. C (1.8%)	*Chaetozone* sp. A[a] (2.5%)	*Prionospio* sp. B (1.7%)
Levinsenia gracilis (2.8%)	*Chaetozone* sp. A[a] (1.7%)	*Leitoscoloplos* sp. B[a](2.5%)	*Ophelina cylindricaudata* (1.4%)

[a] Species observed only in the canyon.

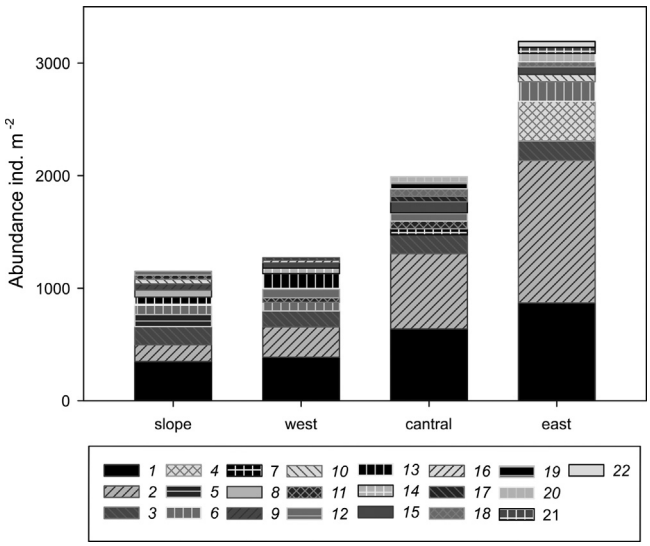

Fig. 2. Composition of the most abundant polychaete species at each of the four study sites. 1, Others; 2, *Paramphinome jeffreysii*; 3, *Aurospio* sp. B; 4, Opheliidae sp. A; 5, *Anguillosyllis capensis*; 6, *Prionospio* sp. I; 7, *Aurospio dibranchiata* 8, *Flabelligella* cf. *biscayensis*; 9, Ampharetidae Genus A; 10, *Glycera capitata*; 11, *Chaetozone* sp. F; 12, *Levinsenia gracilis*; 13, *Ancistrosyllis* sp. A;14, *Leanira hystricis*; 15, *Ophelina abranchiata*; 16, *Chaetozone* sp. C; 17, *Chaetozone* sp. A; 18, *Ophelina cylindricaudata*; 19, Polychaet larva sp. A; 20, *Leitoscoloplos* sp. B; 21, *Aricidea simplex*; 22, *Prionospio* sp. B.

variation in species composition is illustrated in Fig. 2. By far the most abundant species was the amphinomid *Paramphinome jeffreysii* with a total of 2326 ind. m^{-2}, followed by *Aurospio* sp. B (646 ind. m^{-2}), Opheliidae sp. A (393 ind. m^{-2}, represented by juvenile individuals), *Prionospio* sp. I (380 ind. m^{-2}) and *Ophelina abranchiata* (277 ind. m^{-2}). *Paramphinome jeffreysii* increased in relative abundance from 21% in the Western branch to 34% and 40% in the Central and Eastern branches, respectively (Table 2). It was less common at the slope site, where the most abundant species was *Aurospio* sp. B (Table 2). In contrast to *P. jeffreysii, Aurospio* sp. B decreased in relative abundance from west to east (slope 14%, Eastern branch 6%).

There were notable differences in species composition with depth in the sediment profile. The percentage abundance of *Paramphinome jeffreysii* increased into the sediment across all of the sites (Fig. 3). At the Eastern branch, where it was most abundant, *P. jeffreysii* constituted 50% of the polychaete species in the 1–3 and 3–5 cm sediment layers. Juvenile opheliids (Opheliidae sp. A) were particularly abundant (~20%) in the 0–1 cm layer of the Eastern branch.

3.2. Species diversity

Rank 1 dominance differed between sites (Table 1). The Eastern branch had the highest rank 1 dominance (39.7%) and the slope the lowest (18.7%). The *k*-dominance plot (Fig. 4) revealed a similar trend in dominance, highest at the Eastern branch site and lowest at the slope site, with the Western and Central branches having intermediate values.

Simple alpha diversity measures indicated that diversity varied between sites. The average Simpson index ($1-\lambda'$) was highest at the slope site (0.918), intermediate in the Western and Central branches (0.880 and 0.856 respectively) and lowest in the Eastern branch (0.814) (Table 1). The average Shannon index (H' ($\log_2$)) was likewise highest at the slope site (4.104) and lowest in the Eastern branch (3.656). Species evenness decreased from west to east across the sites. The average evenness index (J') was highest on the slope and lowest in the canyon branches (Table 1).

Rarefied polychaete species richness was highest on the slope and all three canyon sites had a similar species richness (Fig. 5a), consistent with hypothesis 3. This pattern was also supported by the Chao 1 indices (Table 1). None of the rarefaction curves reached an asymptote, suggesting that the local diversity was undersampled even when the results were pooled. The higher richness at the slope site was evident from the individual-based (Fig. 5a) rarefaction curves, although confidence intervals overlapped, indicating that the differences were not statistically significant. When all sites were rarefied to 47 individuals, the slope site had the highest species richness (21 species). All three canyon sites had similar predicted numbers of species with $E[S_{47}]$ values decreasing only very slightly (from 20 to 18) from centre to east (Table 4). When all sites were combined (Fig. 5c, Table 4), the expected number of species was lower than at the slope site alone.

3.3. Beta diversity

There is little if any variation in beta diversity within or among the sites studied, whether assessed as Hill number 0, 1 or 2 (Table 4). However, rarefied average α diversity and rarefied γ diversity are all highest at the slope site. Similarly, rarefied average α diversity, and rarefied γ diversity are increased from canyon-level to regional-level measures. The degree of increase appears to be related to the Hill number, least in richness, and greatest in inverse Simpson (i.e. evenness). Taken together, these results suggest both increased richness and reduced dominance at the slope site relative to the canyon sites.

3.4. Multivariate analyses

A non-metric multidimensional scaling ordination of polychaete species data (Fig. 6) revealed appreciable differences in community composition between all four study sites, thereby supporting hypotheses 1 and 2. The Eastern and Central branch sites were most similar to each other. Western branch samples formed a looser grouping, which was nevertheless distinct from those at the other canyon sites. The slope samples grouped together and were distinct from the canyon sites. Global ANOSIM indicated significant variation ($p < 0.001$), with all pair-wise site comparisons significant at $p < 0.01$, except slope and Western branch, which was significant at $p < 0.02$. SIMPER analysis (Table 3) indicated that the abundance of *P. jeffreysii* was responsible for most of the observed similarity within sites. *Aurospio* sp. B abundance was second or third most important at all sites. Between-site dissimilarity was mostly driven by the abundance of *P. jeffreysii, Opheliidae* sp. A (juveniles) and *Ancistrosyllis* sp. A.

Canonical correspondence analysis (Fig. 7) showed the potential interactions between environmental factors and the distribution of polychaete species. Axis 1 was positively correlated with water depth and negatively correlated with macrofaunal density (a potential proxy of organic matter supply, Gunton et al., 2015). Axis 2 was correlated with sediment characteristics, including grain size and slope angle. Species such as *Leanira hystricis, Ancistrosyllis* sp. A, *Sternaspis* sp. A and *Chaetozone* sp. C were characteristic of the deeper and lower macrofaunal density sites in the Western branch (Supplementary Fig. S1). Opheliidae sp. B, *Anguillosyllis capensis* and Scalibregmatidae sp. B were characteristic of the coarser-grained sediment with a higher clay percentage on the slope. Opheliidae sp. A (juveniles), *Paramphinome jeffreysii* and *Leitoscoloplos* sp. B were characteristic of the Eastern and Central branches, which shared similar environmental characteristics.

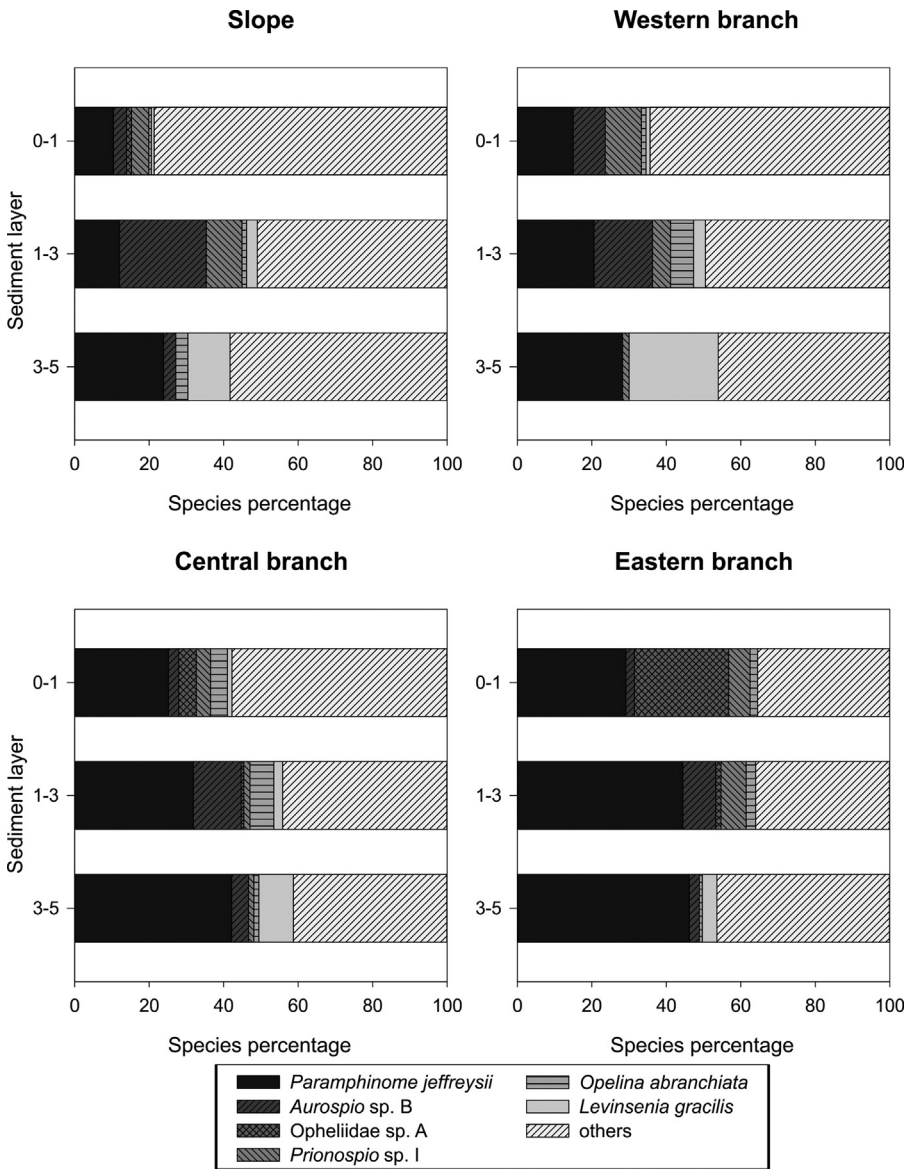

Fig. 3. Vertical distribution of polychaetes in sediments layers (0–1, 1–3 and 3–5 cm) at each site represented as percentage abundance.

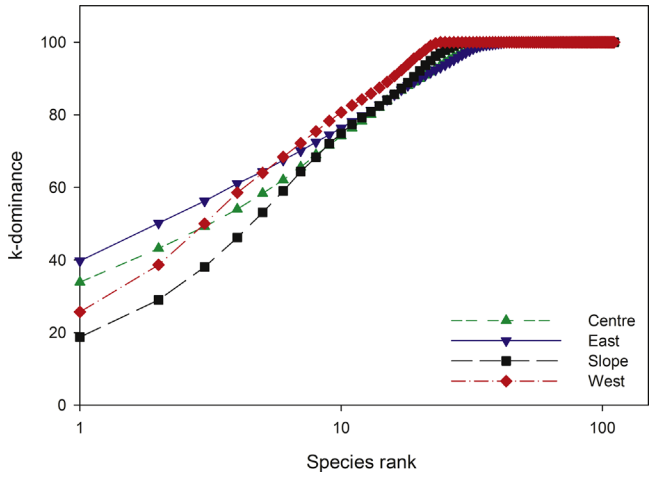

Fig. 4. k-Dominance plot for Whittard Canyon and slope sites, using pooled data from five samples at each of the four sites.

4. Discussion

4.1. Polychaete assemblages

The species composition of the polychaete assemblages differed between branches of the Whittard Canyon, in agreement with hypothesis 1. This is consistent with previous family-level studies of polychaetes in the same canyon system (Hunter et al., 2013; Gunton et al., 2015). Multidimensional scaling and CCA revealed that the Eastern and Central branch species assemblages were closely related (Figs. 6 and 7). Again, this pattern was also observed at the family level and may reflect a combination of similar environmental conditions and geographical proximity (Gunton et al., 2015). The Western branch samples yielded a more distinct assemblage, characterised by *Ancistrosyllis* sp. A (a member of the family Pilargidae), which made up 10% of the polychaete species in the Western branch but was not present in other canyon branches. There is very little information regarding the ecology of the Pilargidae (Fauchald and Jumars, 1979), making it difficult to

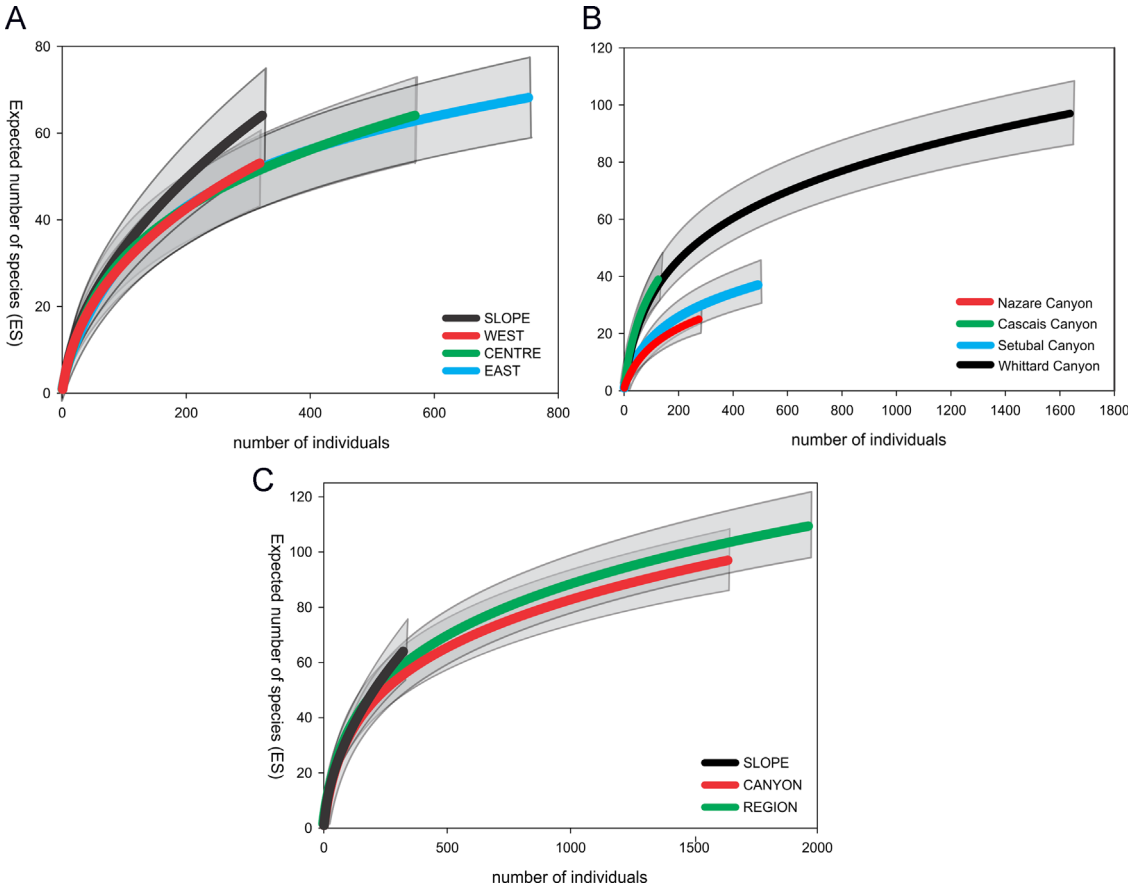

Fig. 5. Polychaete diversity estimated using rarefaction, 95% confidence intervals shown as grey shading. (A) Slope site, Western, Central and Eastern branches. (B) Combined Whittard Canyon branches (Western, Central and Eastern branches) and Iberian Margin canyons (Nazaré, Setúbal and Cascais Canyons) at 3400 m. (C) Combined Whittard Canyon branches, slope site and Whittard Canyon region (Slope site, Western, Central and Eastern branches).

speculate why this species was abundant in the Western branch.

In addition to these intra-canyon patterns, polychaete assemblage composition differed between the canyon branches, as a whole, and the adjacent open slope. This is consistent with hypothesis 2. It also agrees with the findings of De Leo et al. (2014) who recorded a difference in macrofaunal assemblage composition, particularly among polychaetes, between canyon and slope sites in the region of the main Hawaiian Islands. Our CCA results suggest that these species-level differences might be linked to the different sediment characteristics (e.g. coarser-grained sediments on the slope than in the canyon) and increased organic matter input into the canyon branches (Fig. 7). Duros et al. (2011) attributed differences in the benthic foraminiferal species composition between the branches and the slope, at depths comparable to those of the present study, to the preferential deposition of organic detritus in canyon branches.

Paramphinome jeffreysii was the top-ranked species at all sites except the slope site (Table 2). It represented, on average, 31.5% of the total assemblage composition inside the canyon compared with 14.3% on the slope. A SIMPER analysis suggests it was also responsible for much of the similarity between stations inside the canyon and between the canyon and the slope (Table 3). The relative abundance of *P. jeffreysii* increased from west to east, reaching almost 40% of the assemblage in the Eastern branch. It was also more common in the deeper sediment layers (1–3, 3–5 cm) than in the upper 1 cm horizon (Fig. 3). The abundance of this small, omnivorous polychaete (Fauchald and Jumars, 1979) throughout the canyon may indicate an opportunistic response to organic-matter enrichment inside the canyon. Significant

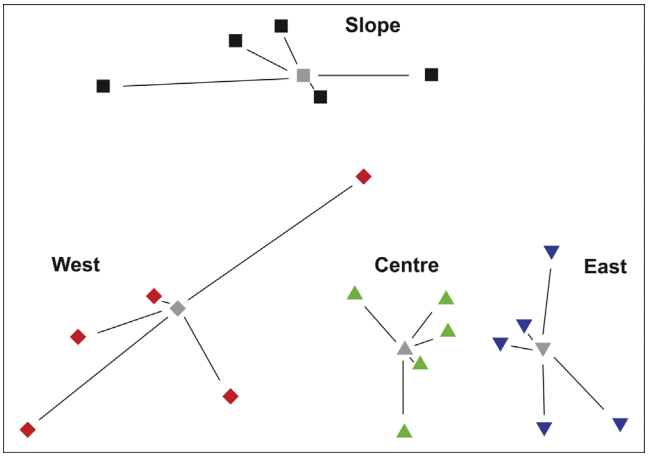

Fig. 6. nMDS ordination plot of polychaete species composition at four study sites (grey symbols represent centroids).

increases in the abundance of the same species in the North Sea have been linked to an increase in food availability (Kroncke et al., 2011). High abundances of *P. jeffreysii* were also associated with organically-enriched sediments near fish farms along the Norwegian coastline (Bannister et al., 2014) and a trough (100 m depth) off the Swedish west coast (Rosenberg, 1995).

Juvenile polychaetes in the family Opheliidae (Opheliidae sp. A) were common in the 0–1 cm layer of samples from the Eastern branch (Fig. 3), where they accounted for 11% of the assemblage and were ranked second after *P. jeffreysii* (Table 2). This too may

Table 3
SIMPER analysis displaying the percentage contribution of the most important species responsible for within site similarity and between site dissimilarity. W – Western branch, C – Central branch, E – Eastern branch, Sl – Slope site.

Similarity between samples within sites (%)			
Sl-average 51.9	**W-average 49.0**	**C-average 61.0**	**E-average 56.1**
Paramphinome jeffreysii-6.7	*Paramphinome jeffreysii*-9.2	*Paramphinome jeffreysii*-11.4	*Paramphinome jeffreysii*-12.0
Aurospio sp. B-6.7	*Aurospio* sp. B-6.8	*Aurospio* sp. B-4.9	Opheliidae sp. A-4.4
Anguillosyllis capensis-5.8	*Ancistrosyllis* sp. A-4.1	*Levinsenia gracilis*-3.5	*Aurospio* sp. B-4.1
Aurospio dibranchiata-4.6	*Chaetozone* sp. F-3.9	*Ophelina cylindricaudata*-3.5	*Prionospio* sp. I-3.7
Flabelligella cf. biscayensis-4.4	*Prionospio* sp. I-3.1	*Chaetozone* sp. F-3.0	*Leitoscoloplos* sp. B-2.9
Dissimilarity between sites (%)			
C&E-average 45.2	**C&Sl-average 57.5**	**C&W-average 55.4**	**Sl&W-average 57.5**
Opheliidae sp. A-2.6	*Paramphinome jefreysii*-3.8	*Paramphinome jeffreysii*-2.7	*Ancistrosyllis* sp. A-3.3
Paramphinome jeffreysii-2.0	*Anguillosyllos capensis*-2.8	*Ancistrosyllis* sp. A-2.5	*Anguillosyllis capensis*-2.4
Prionospio sp. I-1.4	*Ophelina cylindricaudata*-2.0	*Ophelina cylindricaudata*-2.2	Ampharetidae new genus sp. A-2.1
Sl&E-average 61.8	**E&W-average 61.7**		
Paramphinome jefreysii-5.5	*Paramphinome jefreysii*-4.6		
Opheliidae sp. A-3.6	Opheliidae sp. A-4.1		
Leitoscoloplos sp. B-2.0	*Ancistrosyllis* sp. A-2.5		

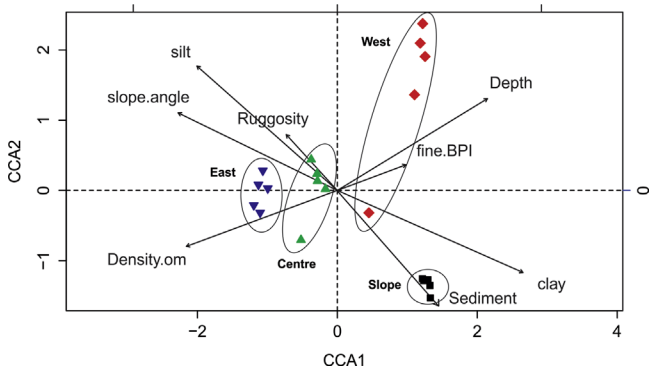

Fig. 7. Canonical correspondence analysis of polychaete species composition at four study sites. Depth=water depth; fine BPI=fine-scale bathymetry position index; clay=percentage clay; Density.om=macrofaunal density as a proxy for organic matter input; slope.angle=slope angle; silt=silt percentage; Sediment=sediment grain size.

indicate a recent input of organic matter onto the sediment surface. During a time-series study at a deeper site (~4850 m), located 464 km to the west of our study area on the Porcupine Abyssal Plain (PAP), morphologically very similar juvenile opheliids were found in high densities in the upper 2-cm layer of multicore samples (Vanreusel et al., 2001). Over the two year study period, a stable population of juvenile Opheliidae displayed a slow increase in the body size (Vanreusel et al., 2001). These opheliids were interpreted as opportunists that had recently been recruited following the deposition of a pulsed input of phytodetritus. A separate contribution to the same time-series study (Soto et al., 2010) also recorded a large increase in the abundance of opheliid juveniles at PAP. Again, this was interpreted as a recruitment event linked to phytodetritus deposition. Studies of shallow-water opheliids suggest that they have an opportunistic life history (Hermans, 1978). Experiments on the continental shelf off North Carolina showed opheliid and capitellid abundance increasing by 2–90 times in enriched sediment trays compared with unenriched trays (Renaud et al., 1999). Population densities of the opheliid *Armandia brevis* from waters off San Juan Island, Washington, fluctuate markedly throughout the year as a result of reproductive events (Woodin, 1974). The opheliids are likely to be opportunists waiting for optimal conditions before converting their energy resources into reproductive effort (Vanreusel et al., 2001). Our observations in the Whittard Canyon suggest that this

Table 4
Assessment of beta diversity via rarefaction with Hill numbers (^{0}D, richness; ^{1}D, exponential Shannon; ^{2}D, inverse Simpson), α rarefied to 47 individuals, and γ rarefied to 235 individuals. β=beta diversity=$\gamma/\bar{\alpha}$. Canyon=all canyon sites. Region=all canyon sites+slope site.

	^{0}D			^{1}D			^{2}D		
Site	$\bar{\alpha}$	β	γ	$\bar{\alpha}$	β	γ	$\bar{\alpha}$	β	γ
West	18.5	2.5	46.1	12.2	1.7	20.2	8.4	1.4	11.5
Centre	19.9	2.3	45.7	11.8	1.5	18.1	7.0	1.1	7.6
East	18.4	2.5	45.9	8.8	1.5	14.5	5.4	1.0	5.6
Slope	21.2	2.6	54.0	15.7	1.6	24.8	11.9	1.3	15.0
Canyon	18.9	2.6	49.0	11.3	1.7	18.7	6.9	1.1	7.5
Region	19.5	2.7	51.8	12.4	1.7	21.1	8.2	1.1	8.7

species enhances the overall reproductive effort compared with the adjacent slope. Indeed, Vetter et al. (2010) suggest that canyons may act as sources for benthic invertebrates in which dense aggregates of individuals reproduce inside the canyons and send their larvae out onto the adjacent continental slope.

It is interesting to note the large depth range (3500–4850 m) of Opheliidae sp. A, which spans both the lower bathyal and abyssal zones in the NE Atlantic. It has been suggested that depth zonation amongst macrofauna is closely related to their dispersal abilities during their early development (Grassle et al., 1979). Assuming they all represent the same species, larvae of the opheliid recognised in the present study may be well adapted to dispersal, allowing them to span a large depth range. All juvenile opheliids in the study of Vanreusel et al. (2001) were presumed to belong to the same species. This species could not be determined as none of the individuals displayed full adult characteristics and all adult opheliids found at the PAP site in previous studies were new to science and not formally identified. The most abundant identified opheliid in our material was *Ophelina abranchiata.* It is not clear whether the juveniles represent this species or a complex of several species. Further work using genetic methods may elucidate this problem.

4.2. Polychaete diversity

4.2.1. Alpha diversity

Polychaete species diversity was similar in the Western, Central and Eastern branches of the Whittard Canyon, with the Western branch samples yielding slightly higher values of H' than the other

two branches (Table 1). Total species numbers (species richness) were highest in the Eastern branch, followed by the Central, and Western branches, consistent with the higher abundances in the Eastern branch. All alpha diversity measures examined (Pielou's evenness J', Shannon index $H'(\log_2)$, Simpson's index $1-\lambda'$, Berger–Parker index (R1D) and the Chao1 asymptotic richness measure) indicated higher diversity (lower dominance) in the slope samples; the canyon samples had both reduced richness and increased dominance relative to the slope samples, consistent with hypothesis 3. Depressed species diversity inside canyons has been noted for macrobenthos in the Nazaré Canyon (Curdia et al., 2004), Scripps and La Jolla Canyons (Vetter and Dayton, 1998) and for polychaetes in the Portuguese canyons (Paterson et al., 2011). A number of ecological studies have suggested a unimodal relationship between diversity and productivity (Rosenzweig, 1995). In oligotrophic settings, diversity increases with increasing food availability to reach maximal values at intermediate levels of productivity. Where levels of food availability are excessive, diversity may be depressed (Levin et al., 2001). In the case of the La Jolla Canyon system, depressed diversity in shallow parts of the canyon was linked to dominance by opportunistic species associated with deposits of kelp and surfgrass detritus (Vetter and Dayton, 1998). In coastal marine systems, increased organic enrichment resulting from pollution can lead to higher infaunal standing stocks, as well as oxygen depletion and dominance by a few hypoxia-tolerant species (Pearson and Rosenberg, 1978). This has also been observed in upper bathyal oxygen minimum zones where dense, high-dominance, low-diversity benthic assemblages are associated with natural organic enrichment (Levin et al., 1994; Levin, 2003; Gooday et al., 2010). However, there is no evidence for organic enrichment from macrophyte detritus, or oxygen depletion, at our canyon study sites.

High levels of physical disturbance inside the canyon may also depress polychaete diversity in accordance with the Intermediate Disturbance Hypothesis (Connell, 1978, Huston, 1979), which predicts maximal levels of local species diversity when disturbance is neither too rare nor too frequent. At the High Energy Benthic Boundary Layer Experiment (HEBBLE) site in the NE Atlantic, disturbance generated by episodic strong currents ('benthic storms') was linked to high species dominance by polychaetes (58-64% ampharetids), bivalves, isopods and tanaids (Thistle et al., 1985). Most of the polychaetes were small and all were sexually immature, suggesting larval recolonisation of defaunated patches created by physical disturbance. Disturbance in the form of high-energy currents was considered important in the structuring of polychaete diversity on the Hebridean Slope in the Rockall Trough (Paterson and Lambshead, 1995). It has been suggested that community disturbance resulting from strong currents, high sedimentation rates and re-suspension may explain the depressed diversity and increased dominance among macrofauna and meiofaunal taxa in the Nazaré (Gage et al., 1995; Curdia et al., 2004; Koho et al., 2007; Ingels et al., 2009) and Setúbal (Gage et al., 1995) canyons. Paterson et al. (2011) attributed the dominance of a *Prionospio* species in the Nazaré Canyon to an opportunistic response to a disturbance event. The disturbance could have been caused by the periodic deposition of organically-enriched sediment, but a spring-tide-mediated turbidite event or increased bioturbation by larger macro/megafauna were also thought possible (Paterson et al., 2011). The lower diversity of sessile and sedentary megafauna in Hawaiian canyons was attributed to periodic disturbances, such as sediment slumps and turbidity currents, although mobile megafauna (e.g. fish and crustaceans) that were able to avoid or tolerate these disturbance events better than less mobile taxa exhibited enhanced diversity inside the canyons (Vetter et al., 2010). The depression in diversity observed at 700 m within the La Jolla Canyon system was also linked to disturbance from strong currents (Vetter and Dayton, 1998).

Polychaete diversity in the Whittard Canyon system is relatively high compared with that in the Nazaré and Setúbal canyons on the Iberian Margin, but similar to levels in the Cascais Canyon (Fig. 5b). Paterson et al. (2011) analysed polychaete diversity in these canyons, in each case at depths of 1000, 3400, and 4300 m. They attributed differences in polychaete rarefied species richness between them to different environmental characteristics. The Nazaré Canyon is active with periodic disturbances and relatively high current speeds (de Stigter et al., 2007; Garcia et al., 2007). Reduced diversity in the middle part of the Setúbal Canyon was attributed to lower productivity. The higher diversity in the Cascais Canyon suggested that it is a more quiescent canyon, where disturbance and productivity effects are balanced (Paterson et al., 2011). If correct, these inferences suggest that the Whittard Canyon is less active than the Nazaré and more similar to the Cascais Canyon, at least around 3400 m in the middle section.

4.2.2. Beta diversity

Levels of beta diversity on the ocean floor are poorly understood and appear to vary between taxa (Ellingsen et al., 2007a). Paterson et al. (1998) reported a difference in the species composition of polychaete assemblages at sites on NE Atlantic and equatorial Pacific abyssal plains separated by 500–1000 km. They suggested that faunal turnover occurred across scales of 1000+km on abyssal plains. Similarly, Glover et al. (2001) reported differences in polychaete species assemblages at four sites in the NE Atlantic (Porcupine, Tagus and Cape Verde Abyssal Plains) that were separated by distances of up to 3300 km. However, our data suggest there is a change in polychaete species composition across the 60 km spanned by our four study sites. It seems likely, therefore, that rates of beta diversity are considerably higher on continental margins dissected by canyons than they are on abyssal plains, which are topographically much less complex and offer fewer barriers to dispersal than the ocean margins.

Another way to assess the change in species composition across the study sites is provided by Whittaker's beta diversity (β_W). According to this metric, there was no clear variation in beta diversity, although we should note that the sample size limitations (minimum number of specimens per sample) may have restricted our ability to detect a change. Our beta diversity assessment (Table 4) nevertheless makes clear the enhanced α and γ diversity levels of the slope site compared with the canyon sites. This meant that all aspects of diversity (^{0}D, ^{1}D, ^{2}D) were reduced when canyon data were added to the slope data.

There was surprisingly little difference in the composition of species assemblages between the slope and the Western canyon branch (Fig. 8). Our canyon samples are all from soft-bottom areas that are not too dissimilar in terms of sediment characteristics from the open slope. However, the Whittard Canyon as a whole encompasses a wide range of different habitats. The head of the canyon is characterised by turbidity currents and oxygen-limited, possibly sulphidic conditions (Ingels et al., 2011). Vertical cliffs (Huvenne et al., 2011) and cold-water corals (Morris et al., 2013; Huvenne et al., 2011; Robert et al., 2014) are present in the upper to mid reaches, flat areas of soft sediment in the thalweg (Robert et al., 2014) and deeper parts of the canyon. Analyses of polychaete assemblages from these different areas inside the canyon would almost certainly increase species-level differences in the assemblages both between canyon and slope and within the canyon and thereby enhance species turnover. McClain and Barry (2010) observed that the highest rate of faunal turnover in the Monterey Canyon off the central Californian coast, USA, was closest to the canyon wall. These authors concluded that the canyon walls enhanced the input of organic debris, which significantly altered the

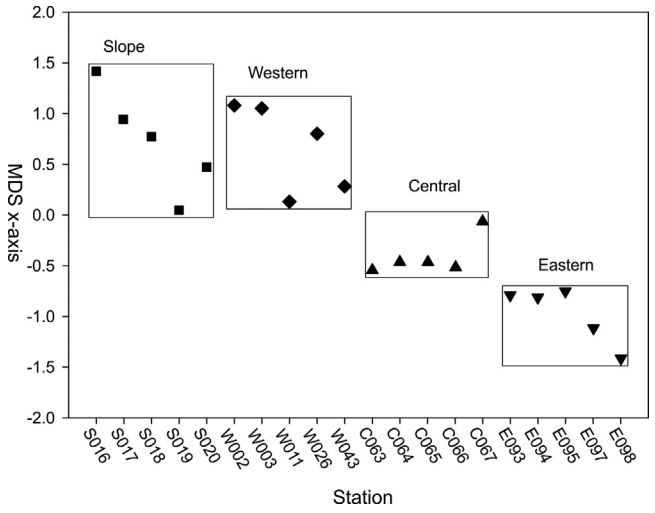

Fig. 8. Plot of nMDS ordination *x*-value against sampling identity for polychaete species composition at four study sites.

benthic assemblages. In the Whittard Channel (a continuation of the canyon system) at 4000–4400 m depth, Amaro et al. (2015) concluded that organic matter enrichment mainly resulted from the concentration within the Channel of phytodetritus deposits derived from surface production during the spring bloom, which occurs in this region from April to May (Joint et al., 2001). Our canyon samples were all collected in June/July, either from within or next to the canyon thalweg. Polychaete assemblage composition, including the high abundance of opportunistic juvenile opheliids and *P. jeffreysii,* may have been influenced in a similar way by the concentration in this depression of detrital material originating from the spring bloom.

4.2.3. Regional species diversity

Continental margins are characterised by high species diversity (Hessler and Sanders, 1967), related in part to the considerable habitat heterogeneity that characterises these regions of the deep sea (Levin and Dayton, 2009; Levin et al., 2010). By virtue of their extreme topography, complex current regimes, and tendency to concentrate organic matter and sediment, submarine canyons make a substantial contribution to this heterogeneity (Vetter and Dayton, 1999; McClain and Barry, 2010). Canyons in the Hawaiian Archipelago were thought to enhance the regional diversity of megafauna with high mobility, with 41 species being only found inside the canyon and not on the slope (Vetter et al., 2010). As noted above, diversity was reduced in the present study when canyon and slope data were combined. Nevertheless, 46 polychaete species were only recorded from the canyon branches, which tends to support hypothesis 4, that canyons increase regional diversity in soft-sediments by harboring species different from those found on the adjacent slope. However, our sampling effort was not equal at the canyon and slope sites (i.e. 15 and 5 samples, respectively) and therefore we do not have enough evidence to conclude that the Whittard Canyon enhances the diversity of benthic polychaetes at regional scales.

4.3. Polychaete biogeography

The 25 species that were found at all four study sites accounted for 72.3% of polychaete specimens. They include the two most abundant species (*Paramphinome jeffreysii* and *Aurospio* sp. B), which made up 39.4% of the total number of identified polychaetes in our samples. On the other hand, the 43 species that occurred at a single site accounted for only 2.9% of all specimens. This pattern is consistent with the observations of Glover et al. (2001), who recognised a core group of polychaete species that were widely distributed at their four NE Atlantic abyssal plain sites. These species represented about 70% of the fauna at the Madeira Abyssal Plain but around 50% or less at three other sites. However, a large majority (81%) of the species they recognised were unique to one of their sites. They attributed the large number of unique species to a vast regional species pool and inadequate sampling effort. Wide spatial distributions of the most abundant species and the apparent compressed range of the least common species were also noted in the case of polychaetes from the Southern Ocean (Ellingsen et al., 2007b). Indeed, this pattern is suggested for many groups of species, habitat types and spatial scales (Brown, 1984).

Some species found in the Whittard Canyon apparently have cosmopolitan distributions on a global scale. For example, there are records of *Aurospio dibranchiata,* which was found at all four of our sites, from the Atlantic, Pacific and Southern Oceans (Smith et al., 2006). With fewer barriers to dispersal in the deep sea, compared with shallow-water habitats, wide dispersal of species might be expected (Grassle and Morse-Porteous, 1987). However, barriers do exist and these are probably more common on continental margins than abyssal plains (McClain and Mincks Hardy, 2010). Despite these restrictions to dispersal, some species do appear to have cosmopolitan distributions in the deep sea, particularly at abyssal depths (Wilson and Hessler, 1987; McClain and Mincks Hardy, 2010; Gooday and Jorissen, 2012). In the case of certain foraminiferal species, this is supported by molecular evidence (Pawlowski et al., 2007; Lecroq et al., 2009). Conversely, some species identified morphologically as 'cosmopolitan' have proved to comprise a complex of cryptic species with smaller ranges when investigated with molecular methods (e.g.,Vrijenhoek et al., 1994; France and Kocher, 1996; Quattro et al., 2001).

Paterson et al. (2011) suggest that canyons may harbour endemic polychaete species. Forty-six polychaete species were found inside the Whittard Canyon branches but not on the adjacent slope. Of these 46 species, 34 could not be assigned a binomial Latin name. Out of the twelve species that could be given a Latin name, one was originally described from the Northeast Atlantic (*Exogone (Parexogone) campoyi*), two from the Northwest Atlantic (*Aglaophamus minusculus*, *Aricidea (Strelzovia) quadrilobata*), three from the Arctic Ocean (*Laonice blakei*, *Micronephthys minuta*, *Pseudoscalibregma parvum*), two from the Norwegian coast (*Ampharete finmarchica, Amphicteis gunneri)*, two from the Californian coast (*Cenogenus fusca* and *Levinsenia oculata*), one from the Southern Ocean (*Augeneria tentaculata*) and one from off the Japanese islands (*Anobothrus patersoni*). None of these species is confined to the broader area around the canyon, although *E. (P.) campoyi* has been recorded only from the Bay of Biscay, the western Mediterranean, and the Aegean Sea. Interestingly, this species was first described from the Capbreton Canyon in the Bay of Biscay (San Martin et al. 1996), suggesting it may be common in canyons.

It is estimated that up to 90% of deep-sea species have not been formally described (Smith et al., 2006) and consequently species distributions are very poorly understood (Glover et al., 2001; McClain and Mincks Hardy, 2010). This applies as much to polychaetes as it does to other deep-sea taxa (Paterson et al., 2011). The prevalence of undescribed species in our samples makes it difficult to determine whether any are endemic to the Whittard Canyon. Two species found in the Whittard Canyon, *Aurospio* sp. B and *Prionospio* sp. I, were also recorded in the Iberian canyons and are currently being described (Paterson et al. submitted). These new species appear to be closely associated with canyons. *Prionospio* sp. I has only been found in canyons (L. Neal unpublished observations). *Aurospio* sp. B has been recorded in a non-canyon environment on the Porcupine Abyssal Plain, but only in very low densities (G. Paterson unpublished observations). Both

may be (Foix, Lacaze-Duthiers and Planier canyons) and are thought to be endemic to either one or multiple Mediterranean canyons (Gili et al., 2000; Bouillon et al., 2000). The life cycles of these endemic hydromedusea are closely linked to factors specific to the canyon environment, such as topography, sedimentation and hydrographic conditions. Similarly, Paterson et al. (2011) suggested that some polychaete species are adapted to the disturbed conditions typical of some canyons rather than being restricted to one particular canyon. Further research on the taxonomy of deep-sea canyon polychaetes, using both morphological and genetic approaches, is required in order to understand endemism in canyons and species connectivity between different canyons.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.bios.2014.05.063.

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